Influences of land use history and short-term nitrogen addition on community structure in temperate grasslands

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1. Introduction

At the regional scale, the pattern of vegetation and the distribution of dominant species are largely dependent on land use history (Foster, 1992; Foster et al., 2002; Neill et al., 2007). Historic land use commonly influences plant community succession (Benjamin et al., 2005; Connell and Slatyer, 1977; Foster, 1992). Altered species diversity and community invasibility are likely result from impacts of land use history (Bonet, 2004; Dutoit et al., 2003; Kulmatiski et al., 2006). Better understanding the effects of land use history on vegetation are critical for interpreting current ecological patterns and developing effective conservation and management strategies (Swetnam et al., 1999). In spite of the importance of land use history, its impacts on plant community are often neglected in semiarid grasslands where plant species and community are sensitive to land disturbance (Zheng et al., 2009; Zhou et al., 2006). Given that previous land use may influence species diversity and dominant life forms of plants (Knapp, 1992; Xu et al., 2010), it is expected that community structure and composition will vary with land use history.

Nitrogen is the most limiting nutrient for terrestrial plants, improved N availability generally influences the community composition and alters vegetation pattern (Duprê et al., 2010; Rajaniemi, 2003; Tilman, 1987). Especially in semiarid area, the grasslands were sensitive to N enrichment (Bai et al., 2008; Yang et al., 2011). Enrichment in N will decrease species richness and density of plant community (e.g., DiTomasso and Aarssen, 1989; Gough et al., 2000; Patrick et al., 2008; Stevens et al., 2004; Yang et al., 2011) and influence the succession of grasslands (Kolb et al., 2002; Tilman, 1987). Furthermore, due to their inherent differences in N use strategies, various plant species and functional groups may show differential growth responses to N enrichment (Xia and Wan, 2008), leading to altered inter-specific competitive relations (Joyce, 2001) and changes in abundance and dominance of difference plant species and functional groups (Niu et al., 2009, 2010; Tilman, 1987). As the main source of N input in semiarid area in north China, airborne N is estimated up to 80—90 kg ha⁻¹ yr⁻¹ (He et al., 2007) and higher N deposition would occur in the future (Zhang et al., 2008). Increasing atmospheric N deposition is influencing the community structure and productivity.
in natural grasslands (Bai et al., 2008; Yang et al., 2011). However, it is still not clear how increased N impacts species composition and community structure in grasslands under secondary succession. Since the limitation of N in semiarid grassland and the higher efficiency in N utilization of grass species relative to other species (Niu et al., 2008; Yuan et al., 2005), it is reasonable to hypothesize that N addition will increase the vegetation coverage and stimulate the dominance of grasses.

In Inner Mongolia in northern China, grasslands represent the natural vegetation type and play important roles in providing ecological services and maintaining sustainable socio-economic development of the local area (Kang et al., 2007). However, the grassland has degenerated seriously since 1950s because of over-grazing and reclamation for farming. The Chinese government carried out policies of abandoning grazing and farming since the end of last century to prevent grasslands from further degradation.

As a result, the natural steppe fenced after overgrazing and the old field grassland succeeding after farmland abandonment are the two most common grassland types in Inner Mongolia. Nevertheless, previous studies in this area mainly focus on the steppe; few studies discussed the old field and compared the two grassland types as well as the same grassland type with different restoration time after disturbance.

In this study, we simulated N deposition by adding N in three grasslands with different land use history and monitored the community structure and species composition in two consecutive growing seasons. We addressed the following specific questions: (1) what are the differences in community structure between grasslands with different land use history? (2) how do community structure and species composition respond to N addition in the short term?

2. Methods

2.1. Study sites and experimental design

The study sites were located in Duolun county (116°17′ E and 42°02′ N, elevation 1324 m a.s.l.), in the typical steppe zone of Inner Mongolia Plateau. This area belongs to a typical agro-pastoral ecotone with semiarid monsoon climate of moderate temperature zone (Fig. 1). Mean annual precipitation is 385.5 mm and mean annual temperature is 2.1 °C, with mean monthly temperature ranging from –17.5 °C in January to 18.9 °C in July. Soil is chestnut (Chinese classification) or Calcis-orthic Aridisol in the US Soil Taxonomy classification.

The traditional land use practices in the study area are livestock grazing and farming. The over-grazing and intensive farming on the regional grasslands since the middle of the last century resulted in severe land degradation and desertification (Liu and Tong, 2003; You et al., 2003). To protect the environment from further degradation, the local government has executed the policies of banning grazing and fallowing of cultivated land since 2000 (Zhou et al., 2006).

In April 2005, three grassland sites (approximately 100 m away from each other) were selected for study based on different land use history: steppe fenced for two years (ST), steppe fenced for five years (SF) and old field fenced for five years (OF). All the sites had different in plant stature, rooting depth, water and nutrient use efficiency; and C:N:P stoichiometry (Bai et al., 2004). Species evenness (E) was used to describe the diversity traits of communities, which were calculated as:

\[
E = \left( - \sum P_i \ln P_i \right) / \ln S
\]

Where \(P_i\) is the relative importance value of species \(i\), \(S\) is the total number of species.

2.2. Plant community measurement

In July 2005 and 2006, plant density, species richness were determined within a permanent quadrat of 1 m x 1 m in each plot. Plant cover was measured within the same quadrat by putting a 1 m x 1 m metal frame with 100 equally distributed grids above the canopy (Dong et al., 1996). For the analysis convenience, species were classified into functional groups on the basis of life form: annuals and biennials (AB), perennial grasses (PG), and perennial forbs (PF), based on life forms. The plant functional groups are different in plant stature, rooting depth, water and nutrient use efficiency, and C:N:P stoichiometry (Bai et al., 2004). Species evenness (E) was used to describe the diversity traits of communities, which were calculated as:

\[
E = \left( - \sum P_i \ln P_i \right) / \ln S
\]

Where \(P_i\) is the relative importance value of species \(i\), \(S\) is the total number of species.

2.3. Statistical analysis

Repeated measured ANOVAs were used to analyse the effects of N addition, land use history and their interaction on community...
structure variables. Means of the main effects were compared using Duncan’s multirange test at \( P < 0.05 \). In order to confirm if compensatory effects exist in the community, Pearson’s correlation analysis was used to examine the relationship of any two functional groups cover. Regression analyses were conducted to determine the contribution of both the functional groups and each individual species to change in community cover. All statistical analyses were fulfilled using SPSS (ver. 13.0) software.

3. Results

3.1. Community interannual variations and differences between grasslands

Significant interannual variations in community structure were found in the study \( (P < 0.01; \text{Table 1}) \). Species richness, evenness, plant density, and cover were 14.0, 0.72, 206.2 individuals m\(^{-2}\) and 55.9% in 2005 and 12.5, 0.68, 244.1 individuals m\(^{-2}\) and 72.3% in 2006, respectively \( (\text{Fig. 2a–d}) \). The community structure varied greatly with different land use history. Across two years and all the N treatments, species richness in the steppe fenced for two years \( (\text{ST}, 14.2) \) and five years \( (\text{SF}, 13.7) \) were significant higher \( (P < 0.01) \) than that in the old field \( (\text{OF}, 11.9) \), although there was no remarkable difference between the ST and the SF. Similarly, plant community cover in the ST and SF were 10.6% and 11.0% (absolute difference) higher \( (P < 0.001) \), respectively, than that in the OF \( (56.6\%) \) across the two years \( (\text{Fig. 2d}) \). Year interacted with land use history to affect community structure variables \( (P < 0.01 \text{ for richness, } P < 0.001 \text{ for others}; \text{Table 1}) \).

3.2. Nitrogen effects on grassland

Nitrogen addition significantly increased plant cover \( (P < 0.001) \) but did not affect species richness, evenness or plant density of community \( (\text{Table 1, Fig. 2a–d}) \). Across three grasslands, N addition at the rate of 5, 10, 15 g N m\(^{-2}\) yr\(^{-1}\) stimulated plant community cover by 12.7%, 19.3% and 22.2% (absolute difference) in 2005, and by 10.4%, 17.7% and 19.2% in 2006, respectively \( (\text{Fig. 2d}) \). There were significant differences in plant community cover between the control and all the N addition plots \( (P < 0.001) \). Significant differences in plant community cover \( (P < 0.05) \) were also found between N addition plots except for between the plots of 10 and 15 g N m\(^{-2}\) yr\(^{-1}\). N addition also caused variations in each individual species cover with different degree \( (\text{Supplementary Table 1}) \).

3.3. Different responses of functional groups

Species richness, plant density and cover of different functional groups varied with year, N addition level and land use history \( (\text{Table 2}) \). For AB, species richness was higher \( (P < 0.001) \) in 2005 (3.3) than in 2006 (2.7), while plant density was lower \( (P < 0.001) \) in 2005 (48.7 individuals m\(^{-2}\)) than in 2006 (97.1 individuals m\(^{-2}\)). For PG, however, species richness and plant density had no difference between the two years. Perennial forbs richness was greater \( (P < 0.05) \) in 2005 (7.3) than in 2006 (6.8). Plant cover in 2005 was higher \( (P < 0.05) \) for AB, but lower \( (P < 0.001) \) for PG than that in 2006. No interannual variation in plant cover was found for the PF.

Nitrogen addition increased cover of PG \( (P < 0.001) \), but had no influence on cover of AB and PF. Species richness, plant density and cover of all the functional groups were remarkably different among land use histories. AB species richness was significant \( (P < 0.001) \) higher in the OF \( (6.7) \) than those in the ST \( (1.3) \) and SF \( (1.0) \), whereas the ST and SF had more PG and PF species than the OF \( (P < 0.001; \text{Table 2}) \). Plant density of AB in the OF was significantly greater than those in ST and SF. However, plant density of PG and PF were lower in the OF than in the other two sites, and the PG density was higher in the ST than in the SF \( (P < 0.01; \text{Table 2}) \). The OF had greater AB cover \( (P < 0.001) \), but lower PG \( (P < 0.05) \) and PF cover \( (P < 0.001) \), although the difference was not significant compared with the SF \( (\text{Table 2}) \). Significantly interactive effects of N and land use history on AB species richness were detected \( (P < 0.05) \).

3.4. Effects of N and land use history on the proportional cover of functional groups

Nitrogen addition increased the proportional cover of PG and AB but decreased that of PF, although it was statistically insignificant. The proportional cover of functional groups varied with land use history. Across all the N addition plots and two years, the proportional cover of AB in the OF \( (23.6\%) \) was significantly higher than those in the ST \( (7.3\%) \) and the SF \( (7.3\%) \) \( (P < 0.001; \text{Fig. 3}) \). The proportional cover of PG in the ST and the SF were 11.1% and 9.5% (absolute difference) higher \( (P < 0.05) \) than that in the SF \( (46.1\%) \), respectively. The proportional cover of PF was also markedly different among the ST \( (35.5\%) \), the SF \( (46.6\%) \) and the OF \( (20.8\%) \) \( (P < 0.001; \text{Fig. 3}) \).

3.5. Relationships between functional groups and regression analyses on functional groups and species with plant community

Pearson’s correlation analyses showed that in the ST, plant density of PF was positively correlated with AB \( (P < 0.001) \) but negatively correlated with PG \( (P < 0.05) \). In addition, plant cover of PF showed a negative dependence upon PG \( (P < 0.001; \text{Table 3}) \). In the SF, species richness of PF linearly increased with PG \( (P < 0.05; \text{Table 4}) \) and PF showed a negative dependence upon PG \( (P < 0.05; \text{Table 4}) \). In the OF, only plant density of AB positively depended on PG \( (P < 0.05; \text{Table 3}) \).

Results of regression analyses showed that 29.2% changes in the community cover in the ST could be ascribed to PG \( (P < 0.001; \text{Table 4}) \), whereas in the SF, species richness of PF linearly increased with PG \( (P < 0.05) \) while plant cover of PG declined with AB and PF \( (both P < 0.01) \). In the OF, only plant density of AB positively depended on PG \( (P < 0.05; \text{Table 3}) \).

In the ST, S. krylovii was the most important species, which caused 12.3% of the variations in community cover \( (P < 0.01; \text{Table 4}) \). In the SF, A. frigida, S. krylovii, and A. cristatum contributed 20.4% \( (P < 0.001) \), 8.5% \( (P < 0.05) \), and 7.2% \( (P < 0.05) \) to the changes in community cover, respectively, whereas A. scoparia explained 14.2% \( (P < 0.01) \) of the variations in community cover \( (\text{Table 4}) \). In the OF, 40.3% \( (P < 0.001) \), 26.8% \( (P < 0.001) \), 26.2% \( (P < 0.001) \) and 9.9% \( (P < 0.05) \) of the changes in community cover could be accounted

### Table 1
Repeated measured ANOVAs results (F-value) on the effects of nitrogen addition and land use history on species richness, evenness, plant density and cover of community.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Richness</th>
<th>Evenness</th>
<th>Density</th>
<th>Cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year (Y)</td>
<td>1</td>
<td>2.057**</td>
<td>15.25***</td>
<td>9.99</td>
<td>97.35***</td>
</tr>
<tr>
<td>Nitrogen (N)</td>
<td>3</td>
<td>0.96ns</td>
<td>1.09ns</td>
<td>0.17ns</td>
<td>27.14***</td>
</tr>
<tr>
<td>Land use history (LH)</td>
<td>2</td>
<td>6.77**</td>
<td>0.37ns</td>
<td>1.79ns</td>
<td>16.17***</td>
</tr>
<tr>
<td>Y ( \times ) N</td>
<td>3</td>
<td>1.65ns</td>
<td>1.71ns</td>
<td>1.15ns</td>
<td>0.16ns</td>
</tr>
<tr>
<td>Y ( \times ) LH</td>
<td>2</td>
<td>5.47**</td>
<td>16.91***</td>
<td>57.60***</td>
<td>8.51***</td>
</tr>
<tr>
<td>N ( \times ) LH</td>
<td>6</td>
<td>1.63ns</td>
<td>1.59ns</td>
<td>0.59ns</td>
<td>2.73**</td>
</tr>
<tr>
<td>Y ( \times ) N ( \times ) LH</td>
<td>6</td>
<td>0.85ns</td>
<td>0.99ns</td>
<td>0.55ns</td>
<td>1.11ns</td>
</tr>
</tbody>
</table>

**, and ***: statistically significant at \( P < 0.01 \), and 0.001, respectively; ns: statistically insignificant.
for by *A. cristatum*, *Artemisia sieversiana*, *A. scoparia* and *Setaria viridis* Beauv., respectively (Table 4).

4. Discussion

The interannual variations in plant community structure observed in this study can be mainly ascribed to the great fluctuation in precipitation between the two years. The year of 2006 was abnormally wet, the precipitation in growing season (May–October) was 387.2 mm; while in 2005, it was 298.2 mm and approached the long-term average. The changed precipitation is likely to result in different response of the community.

The significant differences in species richness and plant cover between sites at both community and functional group levels suggest land use history has profound effects on plant community in temperate grasslands. Dyer (2010) proposed that the current patterns of vegetation could be explained by land use history. Change in historical land use can cause the differences in floristic composition, structure and successional processes of plant community (Dolman and Sutherland, 1991; Dutoit et al., 2003). The previous farming on the steppe almost changes the vegetation entirely, leading to the significant differences in species composition and community structure between old field and the other two steppes even after 5-year fencing for restoration. Agricultural activities are recognized as one of the major threats to biodiversity (Nilsson, 1997; Zechmeister et al., 2003). Species richness will decrease in sites formerly disturbed by cultivation (Dutoit et al., 2003; Koyanagi et al., 2009). In this study, previous farming greatly reduces species richness and plant cover, which could be accounted for by the decreases in PG and PF although there are increases in species richness and cover of AB. Annuals and biennials species are mainly opportunistic plants and can quickly increase in its abundance and cover after farming abandonment (Bonet, 2004). However, they compose minority of community and are sensitive to environment change. AB species may lose more easily than do perennial species and are generally displaced by some highly resilient PG during the course of succession (Bonet, 2004; Linusson et al., 1998). The lower plant diversity in the OF presumably results from two reasons: (1) previous cultivation eliminates most of the pristine species as well as their propagules (Bakker and Berendse

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Richness</th>
<th>Density</th>
<th>Cover</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>AB</td>
<td>PG</td>
<td>PF</td>
</tr>
<tr>
<td>Y</td>
<td>1</td>
<td>17.46***</td>
<td>0.56 ns</td>
<td>0.05*</td>
</tr>
<tr>
<td>N</td>
<td>3</td>
<td>1.26 ns</td>
<td>1.73 ns</td>
<td>0.94 ns</td>
</tr>
<tr>
<td>LH</td>
<td>2</td>
<td>356.91***</td>
<td>56.86***</td>
<td>59.52***</td>
</tr>
<tr>
<td>N × LH</td>
<td>6</td>
<td>2.85*</td>
<td>1.23 ns</td>
<td>1.69 ns</td>
</tr>
<tr>
<td>Y × N</td>
<td>3</td>
<td>0.67 ns</td>
<td>1.55 ns</td>
<td>1.10 ns</td>
</tr>
<tr>
<td>Y × LH</td>
<td>2</td>
<td>9.15***</td>
<td>1.19 ns</td>
<td>1.26 ns</td>
</tr>
<tr>
<td>Y × N × LH</td>
<td>6</td>
<td>1.33 ns</td>
<td>0.63 ns</td>
<td>1.76 ns</td>
</tr>
</tbody>
</table>

*, **, and ***: statistically significant at P < 0.05, 0.01, and 0.001, respectively; ns: statistically insignificant.
The variation in the proportional cover of functional groups among satory mechanisms exist in the two grasslands, whereas no nega-
cover between PG and AB, PF in the SF suggest that the compen-
alum between PG and PF in the ST, and of plant density between PG and PF in the OF; old field fenced for five years. AB: annuals and biennials; PG: perennial grasses; PF: perennial forbs.

Species composition and diversity have proven to be significant determinants of processes and function of grassland ecosystems (Chapin et al., 2002; Tilman et al., 1997). Species diversity influences the resilience and resistance of ecosystems to environmental change (Chapin et al., 2000). The relatively more AB species but less species richness, and absence of compensatory effects in the OF indicate its lower ecosystem stability than the ST and SF. This is in accordance with our previous study (Xu et al., 2010). It will take long time for the OF to restore its ecosystem function and stability to the level before farming. More attention should be paid to the functional groups or individual species that account for important change of community cover in grassland management. For example, in the ST, PG, especially S. krylovii is the principal species related to community cover change. Perennial forbs, such as A. frigida and A. scoparia contribute to most proportion of change in community cover in the SF. In the OF, PG, especially A. cristatum, account for about half of the variation in community cover.

The effects of N on plant community will be mediated by water availability in semiarid grassland (Niu et al., 2008; Yang et al., 2011). The change in precipitation is likely to influence the effects of N addition. To avoid the probable impacts of interannual variation in precipitation on N treatment effects, we calculated the relative changes of community parameters respond to N addition within each year. The results suggested that N addition promoted plant community cover as well as the cover of PG in both years, which is consistent with previous studies (e.g., Mountford et al., 1993; Stevens et al., 2006). However, we found no changes in species diversity and plant density under improved N availability. It agrees with Wijesinghe et al. (2005) who proposed that N addition did not affect species richness. Mountford et al. (1993) found there was no remarkable variation in species richness at an application of 25 kg N ha\(^{-1}\) yr\(^{-1}\), but specie richness decreased when 50 kg N ha\(^{-1}\) yr\(^{-1}\) were applied for 3 years. Gross et al. (2005) have demonstrated that increased N had a positive effect on species richness initially, but the effect was either negative or neutral by the third year. These findings suggest the influence of N addition on community was closely related to N amount and the response time of vegetation to N addition. The effect of N addition on plant community also depends on soil water, and the two factors can co-limit plant community in arid or semi-arid grassland (Harpole et al., 2007; Hooper and Johnson, 1999; Kirchner, 1977). The less effects of

### Table 4

<table>
<thead>
<tr>
<th>Sites</th>
<th>Regression equations</th>
<th>R(^2)</th>
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<tbody>
<tr>
<td>Functional groups</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ST PG</td>
<td>y = -0.45x + 46.93</td>
<td>0.292***</td>
</tr>
<tr>
<td>SF AB</td>
<td>y = -0.89x + 71.85</td>
<td>0.143**</td>
</tr>
<tr>
<td>PG</td>
<td>y = 0.32x + 55.77</td>
<td>0.123***</td>
</tr>
<tr>
<td>PF</td>
<td>y = -0.51x + 48.93</td>
<td>0.314***</td>
</tr>
<tr>
<td>OF PG</td>
<td>y = 0.78x + 29.90</td>
<td>0.433***</td>
</tr>
<tr>
<td>PF</td>
<td>y = 0.51x + 49.81</td>
<td>0.137***</td>
</tr>
<tr>
<td>Individual species</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ST Stipa krylovii</td>
<td>y = 0.29x + 59.59</td>
<td>0.129**</td>
</tr>
<tr>
<td>SF Artemisia frigida</td>
<td>y = -0.50x + 58.53</td>
<td>0.204***</td>
</tr>
<tr>
<td></td>
<td>y = -0.89x + 71.62</td>
<td>0.142**</td>
</tr>
<tr>
<td></td>
<td>y = 46.52e0.11</td>
<td>0.085*</td>
</tr>
<tr>
<td></td>
<td>y = -0.72x + 34.12</td>
<td>0.403***</td>
</tr>
<tr>
<td></td>
<td>y = -4.4147x + 61.715</td>
<td>0.268***</td>
</tr>
<tr>
<td></td>
<td>y = -0.13x(^2) + 3.68x + 45.95</td>
<td>0.262***</td>
</tr>
<tr>
<td></td>
<td>y = -2.02x + 51.63</td>
<td>0.099**</td>
</tr>
</tbody>
</table>

*, **, and ***: statistically significant at the 0.05, 0.01 and 0.001 level, respectively.

### Table 3

<table>
<thead>
<tr>
<th>Sites</th>
<th>Regression equations</th>
<th>R(^2)</th>
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<tbody>
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<td>ST</td>
<td></td>
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<tr>
<td>SF</td>
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</tr>
<tr>
<td>OF</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1, **, and *** indicate correlation is significant at the 0.05, 0.01 and 0.001 level (2-tailed), respectively.

1999; Walker et al., 2004) and makes the recruitment discontinu-
ous; (2) historical farming takes away too much nutrition in soil by harvesting crops and makes the soil too infertile to sustain high species diversity at the early stage of secondary succession. Bai et al. (2004) suggested that compensatory effects would take place when the negative correlations existed between certain plant functional groups or species in a community. The markedly negative corre-
lations of plant density between PG and PF in the ST, and of plant cover between PG and AB, PF in the SF suggest that the compensatory mechanisms exist in the two grasslands, whereas no negative correlations was found between functional groups in the OF. The variation in the proportional cover of functional groups among sites suggests the prominent effects of land use history on species composition, which agree with the results by Dutoit et al. (2003).
N addition on species diversity and plant density are possibly because the exquisite drought in the study area limited N transfer from soil to plant roots. Although 2006 was a relatively wet year, the lagged responses of vegetation to N addition may exist, so the remarkable N effects on species composition and diversity were not detected. However, a trend of increase in proportional cover of PG and AB but decrease in that of PF was found in N addition plots. Given that remarkable reductions in plant species richness under long-term N deposition (Clark and Tilman, 2008), we predict the significant N effects on plant community composition and diversity may be found several years later. The accelerated atmospheric N deposition will enhanced the dominance of grasses in semiarid grassland and alter the community structure in the long term.

The historical land use determined the species composition and community structure. Natural successions from farmland to grassland take so long that former arable land can be recognized decades or centuries after abandonment (Dutoit and Alard, 1995; Foster et al., 2003; Wells et al., 1976). Therefore, it must be cautious in reclamation on grassland on account of its negative effects on species diversity and community stability. Taking the far-reaching influences of land use history into consideration, together with insignificant effects of N addition on species diversity and community structure observed in this study, long-term observations are needed to further confirm the influences of N addition and land use history on temperate grasslands, and provide valuable information for grassland conservation and model projections of ecosystem succession under global scenarios of N deposition in semi-arid areas.

Acknowledgements

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jareenv.2012.07.008.

References


